The distribution of Palaearctic Diamesinae

(Insecta, Diptera, Chironomidae)

By **Bruno Rossaro**

The distribution of Palaearctic Diamesinae is analysed and discussed in relation to the phylogenetic tree of the subfamily. The presence of many widespread taxa and the uncertainty about the phylogenetic relationships is an hindrance to formulate zoogeographic hypotheses. The different distribution of tribes Protanypini and Boreoheptagyini is attributed to a vicariance phenomenon. Southern territories of Palaearctic are considered better candidates than the northern ones as centres of origin of some species group.

Prof. B. Rossaro, Department of Biology, Section Ecology, University of Milano, via Celoria 26, I-20133 Milano, Italy.

Introduction

The aim of this study is to analyse the geographic factors responsible of the actual distribution of Palaearctic Diamesinae. Chironomidae are considered a good material for zoogeographic studies (Brundin 1966), but this is true with some reservation. The reasons are listed below.

1. Many species are widespread, because of their very effective dispersion means and their wide ecological niche. Only species that are restricted by their limited dispersion means (e.g. reduced wings) and their narrow ecological niche (e.g. cold-stenothermal species) are good zoogeographic material; this requirement is fulfilled by the subfamily Diamesinae, whose members are all more or less cold-stenothermal (only *Potthastia* and *Sympotthastia* are eurythermal within the subfamily).

2. Vicariance between tribes or genera of Chironomidae is a well known phenomenon when large geographical regions (south America, south Africa, Australia etc.) are considered. Examples of vicariance of species belonging to the same species-group within the subfamily of Diamesinae are known within a single zoogeographical region: a boreo-alpine disjunction is observed within the Palaearctic region (Thienemann 1950), but new evidence had often falsified previous knowledge. It is the case of *Diamesa lindrothi* and *D. latitarsis* (Serra-Tosio 1973): the former is not restricted to the Arctic region, but it is also present in a few stations in the Alps, the latter is not confined in the Alps as previously stated, but it is also present in the Arctic region.

3. Palaearctic genera of Chironomidae are widespread in the region and many genera are also Holarctic. Widespread condition is still observed at the species level, even if endemic species do exist. Progress in knowledge has emphasised in the past that a restricted species distribution is often a mismatch due to the lack of knowledge: *D. veletensis* for example was known to occur only in the Sierra Nevada (Spain), but was later captured in Morocco and in Mongolia (Serra-Tosio 1983).

The aim of the present paper is to try to answer to the following questions:

1. Is the present information available about the distribution of Diamesinae enough to make hypotheses about the historical factors responsible of their distribution, to build area cladograms and to suggest vicariance phenomena within the Palaearctic region?

2. Can the ordination with multivariate methods made on the basis of the species distribution in provinces be useful to suggest hypotheses about point 1.?

Material and methods

Data were filed using the information present in the Catalogue of Palaearctic Diptera (Ashe & Cranston 1991). The Palaearctic region is divided into areas that are called provinces in the present study, they correspond more or less to the political states. The ex-Soviet Union is divided into provinces as described by Soós & Papp (1991). Holarctic species are included in the present data base and their presence in the Nearctic region is given. Presence in provinces that occur near the boundaries of the Palaearctic region is also given. The abbreviations used in data analysis are in Tab. 1.

The distribution of species was analysed by visual inspection, to suggest preliminary hypotheses.

The COMPONENT program was used (Page 1993) to analyse species groups, for which a cladogram of phylogenetic relationships is available (Serra-Tosio 1973). COMPONENT attempts to construct area cladograms using the information given by the known phylogenetic relationships between species and species distribution in provinces. The interpretation of the results outcoming from this program was hindered by the presence of many widespread taxa, that determined duplications of area cladograms when one attempts to reconcile taxon trees with area cladograms.

With the aim to suggest hypotheses about the history of distribution of widespread taxa, data were processed using the CANOCO program (Ter Braak 1988, Ter Braak & Prentice 1988). Different methods were considered because previous knowledge was not available with these data and no "a priori" model could be suggested. Indirect gradient analysis was carried out to discover the most relevant provinces and species gradients, principal component (=PCA) and correspondence analysis (=CA) were considered to analyse both a linear and a gaussian response model. A detrended correspondence analysis (=DCA, detrending by segments) was also carried out.

Direct gradient analysis (constrained ordination) was run using latitude and longitude of the investigated provinces as constraining variables. Constrained ordination also considered both a linear (redundancy analysis = RDA) and a gaussian (canonical correspondence analysis = CCA) response model.

Results

According to Hennig (1966) the primitive (plesiomorph) species of a monophyletic group lives in an area that is expected to be the centre of origin of the group: the progression rule states that a transformation series of characters would run parallel with progression in space (Humphries & Parenti 1986), so the most derived (apomorph) species live in the geographical periphery of the group. The analysis of the distribution must take into account the phylogenetic tree of the Diamesinae (Serra-Tosio 1973). The tree of the tribes and genera within the subfamily is in Fig. 1, the tree of the genus *Diamesa* is in Fig. 2. It must be emphasised that phylogenetic relationships are only tentative, so the analysis of taxa distribution cannot unequivocally bring to the discovery of the centre of origin.

Tab. 1. List of provinces in which the Palaearctic region is divided, and abbreviations (after Soós & Papp 1991).

A	Austria	AL	Albania	B	Belgium	BG	Bulgaria
CH	Switzerland	CS	Czechoslovakia	CY	Cyprus	D	west Germany
DDR	east Germany	DK	Denmark	E	Spain	F	France
FL	Liechtenstein	GB	Great Britain	GR	Greece	H	Hungary
I	Italy	IRE	Ireland	IS	Iceland	L	Luxembourg
M	Malta	N	Norway	NL	The Netherlands	P	Portugal
PL	Poland	R	Roumania	S	Sweden	SF	Finland
TR	Turkey	YU	Yugoslavia				
NET	north Russia	CET	Central Russia	SET	south Russia	TC	Transcaucasus
SMA	Middle Asia	KZ	Kazakh	WS	west Siberia	ES	east Siberia
FE	Far east Siberia	Jap	Japan	Can	Canada	Gree	Greenland
USA	United States						

Boreoheptagyini

Diamesini

Pagastia

Pseudodiamesa

branickii

nivosa

Pseudokiefferiella

Syndiamesa

nigra

edwardsi

hygropetrica

Lappodiamesa

Diamesa *

zavreli

Sympotthastia

macrocera

spinifera

montium

iberica

Potthastia
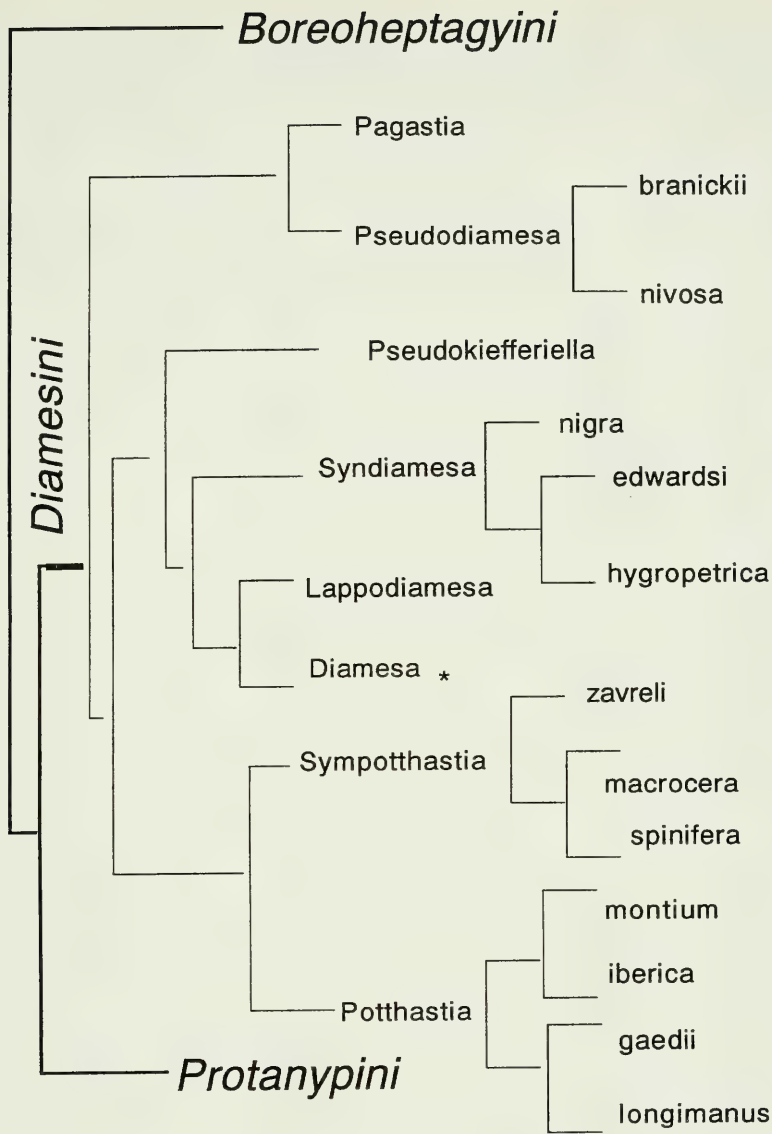
gaedii

longimanus

Protanypini

Fig. 1. Phylogenetic tree of the tribes and genera within the subfamily Diamesinae.

Palaearctic Diamesinae are divided into 3 tribes: Boreoheptagyini, Diamesini, and Protanypini. Boreoheptagyini belong to the Heptagyiae, that with the austral tribes Heptagyini and Lobodiamesini are considered the plesiomorph sister group of Diamesae, that include Harrisonini, Diamesini, and Protanypini (Serra-Tosio 1973, Brundin 1966). It's a snap, that Boreoheptagyini and Protanypini are not widespread on all the territory of the Palaearctic region: the former are absent in the British Isles and in Scandinavia (Serra-Tosio 1989), the latter are absent in the Mediterranean region. The observed distribution cannot be accounted for ecological factors.

When the distribution of genera and species is analysed within the tribe Diamesini, it appears that *Pagastia* is restricted to Siberia and Canada (Beringia), *Pseudodiamesa* is Holarctic, *Pseudokiefferiella* is absent from the south of Europe (in Italy it is restricted to the Alps), but it is present in Nearctic. *Syndiamesa* has endemic species with a very restricted distribution in Europe or in far east of Siberia
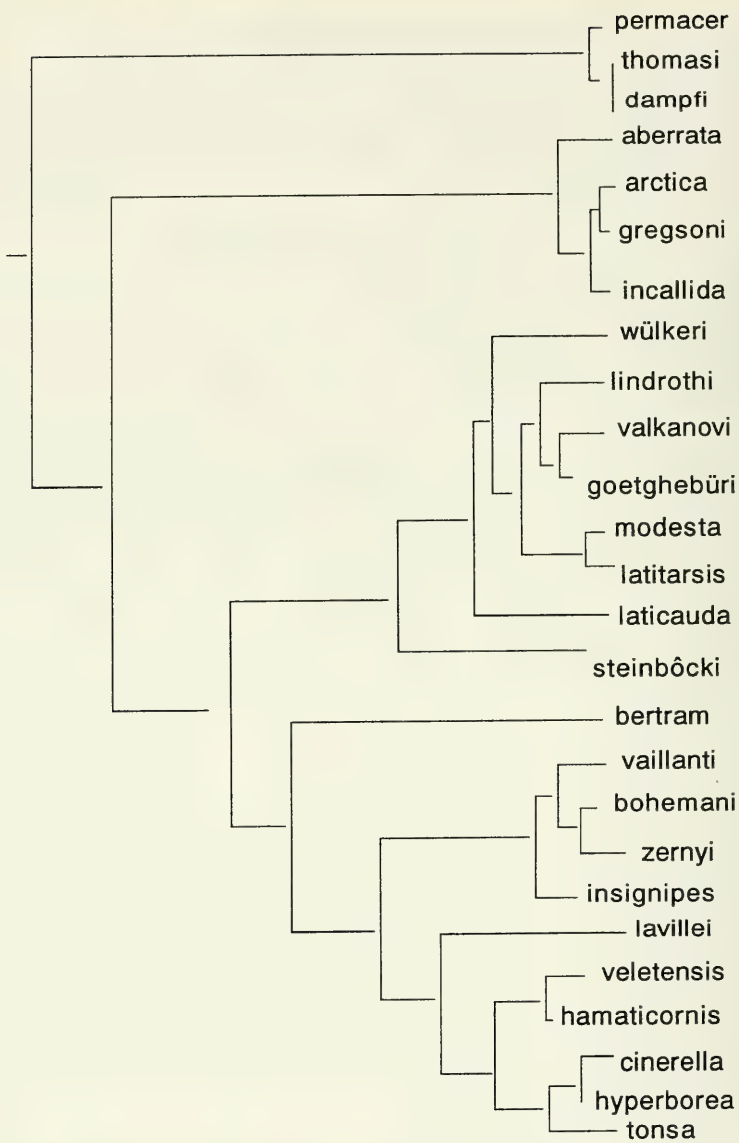
Fig. 2. Phylogenetic tree of the genus *Diamesa*.

(FE); it is also present in Nearctic, but no *Syndiamesa* species is at present known from Scandinavia. *Lappodiamesa* is considered by Serra-Tosio (1973) the plesiomorph sister group of *Diamesa*, it has a restricted northern distribution (eastern Nearctic, Lapland, Novaya Zemblya, FE). *Diamesa* is widespread in the Holarctic. If the distribution of Palaearctic species is examined, within the *dampfi*-group the plesiomorph species *D. permacra* is present both in the Alps and in Scandinavia, whereas the apomorph species *D. thomasi* and *D. dampfi* are absent from Scandinavia. In the *aberrata*-group both the plesiomorph *aberrata* and the apomorph *incallida* are widespread, whereas *arctica* and *gregsoni* are restricted to the northern provinces. Within the *latitarsis*-group the plesiomorph *D. wülkeri* is restricted to the Alps, *D. lindrothi* is common in north Europe and in Greenland, *D. latitarsis* is common in the Alps, present in Scandinavia and Balkan. Within the *zernyi*-group *D. vaillanti* and *D. zernyi* are present in the Pyrenean and in the Alps, *D. bohemani* lives in Scandinavia and in the British Isles. Serra-Tosio (1973) analysing the *cinerella*-group concluded that the plesiomorph species live in south-west Europe, the

apomorph ones in the north-east (*D. hyperborea*, = *D. ursus* lives in Norway). Spain, France and SET are candidates as centres of origin of the group, because they are inhabited by *D. lavillei*, the most plesiomorph species of the group. *D. veletensis* and *D. hamaticornis* are also present in Spain. The capture of *D. veletensis* in Mongolia suggests that many species can have a distribution area that is much more extended than suspected.

Tab. 2. Geographic regions scores in detrended correspondence analysis.

N	NAME	AX1	AX2	AX3	AX4
	EIG	0,436	0,2512	0,1964	0,1454
1	AL	2,1075	0,8686	1,3286	0,6801
2	Afghan	2,5435	0	2,0237	0
3	Alger,	2,0061	0,4437	0,5115	1,4287
4	A	0	1,3968	0,9836	0,7694
5	Azores	2,5854	0,4365	0,1265	1,3268
6	BG	1,442	0,5173	0,5614	1,5539
7	B	2,1635	1,0246	1,3293	0,8885
8	CET	1,9268	0,9933	1,5356	0,4442
9	CH	0,7613	0,9285	0,5464	0,7247
10	CS	1,5985	0,8764	1,506	0,8736
12	DDR	2,0051	0,7818	1,4357	0,5919
13	DK	2,2814	0,7511	1,33	0,6969
14	D	0,4859	1,0934	1,6646	0,9175
15	ES	2,8696	1,6267	1,5029	1,5288
16	E	0,8106	0,2693	1,6258	1,7326
18	F	0,0609	0,6545	1,6606	0,979
19	GB	1,0957	1,0559	1,8032	0,418
20	GR	0,9417	0,9753	1,0442	1,1169
21	Green,	1,5892	1,8184	0,4059	1,0207
22	H	1,7138	0,8601	1,5247	0,6735
23	IRE	1,3611	1,2988	1,6451	0,3516
24	IS	1,0912	1,5205	1,003	0,8054
25	Indiax	1,9634	1,0226	0,656	1,2843
26	I	0,3849	1,2356	1,3884	0,6298
27	J-Kash	1,976	0,9268	0,8115	1,3772
30	Madei,	2,2784	0,1875	0	1,5399
31	Mongol	2,4967	1,3823	2,1745	1,9408
32	Moroc,	1,3868	0,398	1,4215	1,6046
33	NET	2,0619	1,4441	1,3341	0,9346
34	NL	2,1899	0,6836	1,5012	0,7245
35	Nepalx	2,7584	0,4237	1,6079	0,3674
36	N	1,0606	2,451	1,1923	0,3827
37	PL	0,3886	0,7894	1,1201	1,2049
38	Pakist	2,1048	0,9385	1,0027	0,9226
39	R	1,3108	1,1442	0,73	0,9515
40	SET	0,9956	0,0271	1,1806	1,9852
41	SF	1,495	1,899	1,3266	0,6756
42	SMA	3,1307	0,4337	1,0063	0,5979
43	S	1,12	2,3823	1,446	1,2337
45	TR	1,5087	0,6619	0,4722	1,5397
47	WS	2,7408	1,4885	1,2038	1,32
48	YU	1,3939	0,2371	1,6524	0,4043

To sum up many groups have the plesiomorph species with a prevalent Alpine distribution, but there are also situations in which the plesiomorph species live in Scandinavia or in the British Isles. The most frequent condition seems to be the plesiomorph taxon in the Alps, the apomorph one in north Europe. There are also cases in which the taxon has an east Asian-west N. America (=Beringian) distribution *(Pagastia)* and cases where the plesiomorph species within a genus are distributed in west Europe *(Sympotthastia zavreli, Potthastia montium, P. iberica)* whereas the apomorph species extend eastwards *(S. spinifera, P. longimanus)*.

The scores of provinces and species were calculated using PCA, CA, DCA, RDA, and CCA. Scores calculated using DCA are reported in Tab. 2.

Constrained ordination (RDA and CCA) will not be discussed further in this paper because constrained axes have a rather low eigenvalue and the first unconstrained axis (the 3rd in this case) has about the same eigenvalue of the first axis in the unconstrained ordination (Tab. 3). DCA gave better results than CA in the sense that sites ordination given by DCA can be better interpreted.

The first axis calculated with all methods is only roughly related to an west-east gradient, but this is bound to the large difference in species composition between Japan, Siberia, and Europe. PCA emphasises a north-east south-west gradient plotted in the plain of the first two axes, provided that only main trends be considered. All multivariate methods separate Japan from all the other provinces: its dissimilarity from all the other countries is probably exaggerated from the fact that different names had been given to the same species, but this requisites documentation. For this reason Japan was disregarded from data analysis. FE (far east Siberia), Transcaucasia (TC), and Lebanon (Leb) were also excluded because of the high scores in the first (FE) and in the second axis (TC and Leb) in CA analysis. USA and Canada were excluded because they are not Palaearctic. A DCA with the reduced set of data was carried out (DCAR) and results are given in Tab. 2 and in Fig. 3.

The longitudinal gradient cannot be evidenced within the European provinces: for example in DCAR the European provinces are ordered along the first axis in the following sequence: France, Poland, Germany, Spain, and Great Britain (Fig. 3 and Tab. 2). A north-south latitude gradient is outlined in the second axis of DCAR. Scandinavian countries have positive scores and are well separated from the Alpine and Mediterranean countries that have low scores, but ordination again is not strictly following the geographic gradient: Spain has a lower loading than Morocco for example.

DCAR gives high scores in the first axis to the east provinces. It also emphasises the difference between the Arctic and the Alpine fauna: *Boreoheptagyia rugosa, B. cinctipes, Diamesa vaillanti* have very low scores on the first DCAR axis and are endemic in the Alps or in Corsica. Species with high scores in the second axis are Arctic species *(Protanypus caudatus, P. morio, Lappodiamesa brundini)*, whereas species with a low score in the second axis are characteristic of the Mediterranean area *(D. thomasi, Syndiamesa vaillanti)* or of the Oriental region (Afganistan, Nepal) *(D. filicauda, D. löffleri)*. East provinces has high score in the first axis (Figs 3-4).

Discussion

Both ecological and geographical factors must be considered in analysing species distribution. Water temperature and oxygen content are the ecological factors that control Diamesinae species distribution above all. Diamesinae are cold-stenothermal and are restricted to mountain streams, springs, lakes. Species belonging to the *Diamesa latitarsis*-group live only in very cold waters. Species belonging to the

Tab. 3.   Eigenvalues using different multivariate methods.

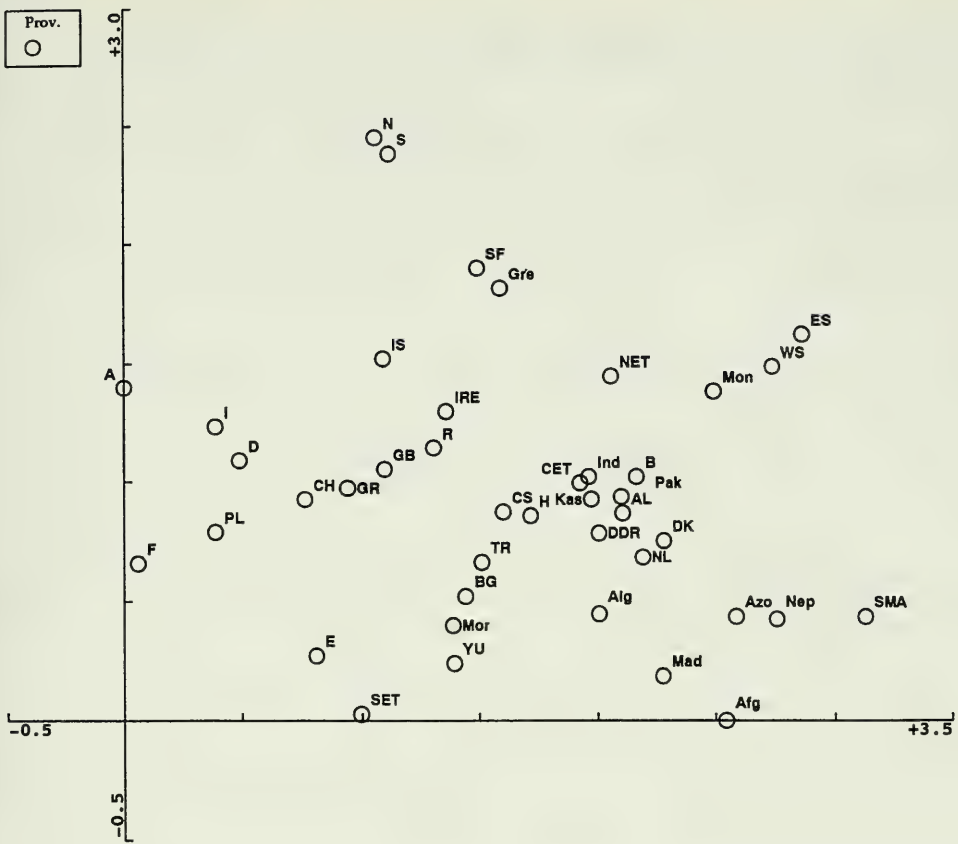| Eigenvalues	axis I	axis 2	axis 3	axis 4
PCA	0,22	0,11	0,08	0,07
CA	0,62	0,44	0,39	0,37
DCA	0,63	0,36	0,24	0,21
RDA	0,05	0,03	0,20	0,09
CCA	0,29	0,22	0,52	0,41

Fig. 3. Detrended correspondence analysis results, provinces scores; abscissa 1st axis, ordinate 2nd axis; abbreviations see Tab. 1.

genus *Potthastia* live in lower stretches of rivers because they tolerate warmer water temperature. Historical that is zoogeographical factors must be considered, when different species occupy a similar niche in different geographic regions. Each geographic district considered in the present study includes different habitats, so ecological factors should not influence so much the observed distribution. Notable exceptions could be Belgium, Netherlands, Denmark that are poor in mountains against Austria and Switzerland that are rich. These provinces are not widely separated in the ordination diagram, emphasising that ecological factors are not relevant in the present study (Fig. 3).

The development of knowledge about species distribution is quite different in different provinces: the Alps are very well studied, whereas Siberia is very poorly known. The uncertainty about phylogenetic relationships between taxa is still strong: the relations between genera within the tribe Diamesini are not well established. The positions of *Pagastia*, *Pseudodiamesa*, *Lappodiamesa*, *Sympotthastia*, and *Potthastia* is particularly uncertain and are probably different from the one proposed by Serra-Tosio (1968, 1973) and reported in Fig. 1. Sæther & Willassen (1988) suggest that the 5 genera are more related to each other than to *Diamesa*. *Lappodiamesa* should be placed differently in the phylogenetic tree: its relation with *Pseudodiamesa* is surely more strict than with *Diamesa*, because of the synaphomorphy represented by the presence of seven elongate scales in the larval pecten of epipharyngis. These are a serious drawback in the formulation of zoogeographic conclusions.

Brundin (1966) was convinced that Chironomidae have a history that goes far back into the Jurassic and that the bipolar distribution pattern is a consequence of a transtropic dispersal northwards.

Serra-Tosio (1973) attempted to explain the geographic distribution of Diamesinae according to the Hennig (1966) and Brundin (1966) principles of systematic phylogenetic and vicariance biogeography.

Fig. 4. Detrended correspondence analysis results, species scores; abscissa 1st axis, ordinate 2nd axis; abbreviations of genera names: B: *Boreoheptagyia*; Prot: *Protanypus*; Pag: *Pagastia*; Ps: *Pseudodiamesa*; D: *Diamesa*; S: *Syndiamesa*; Pseudo: *Pseudokiefferiella*; Pott: *Potthastia*; Smpt: *Sympotthastia*; M: *Monodiamesa*; P: *Prodiamesa*.

The centre of origin of Diamesini was supposed to be in south Africa. The tribe was considered of Gondwanian origin, because Harrisonini, the plesiomorph sister group of Diamesini, are endemic of south Africa. East African mountains were suggested to be the principal way in which ancestral Diamesini reached Europe and north America by dispersion: this event should have happened in Miocene-Pliocene. The absence in the east Africa mountains of plesiomorph species was interpreted as the result of extinction, in other words Laurasia was supposed to be colonised by dispersion from south to north. The presence of fossils of Chironomidae in northern latitudes since the Jurassic-Cretaceous time (Kalugina 1976) does not support this hypothesis, even if it does not contradict it, because the presence of fossils of Diamesini is not unequivocally demonstrated in the northern regions during Jurassic. Willassen & Cranston (1986) are convinced that it is more likely that African species arrived in recent times (mid Tertiary) following an high altitude dispersal route from Europe to Africa, that is from north to south. This is supported by the fact that ecological conditions were suitable in the mid Tertiary for dispersal from north. If Diamesini are of northern origin, it is expected that Diamesini actually discovered in regions that are of Gondwanian origin be more related to the Laurasian ones than to each other. The problem is to demonstrate a very ancient presence of Diamesinae in the northern hemisphere.

Humphries & Parenti (1986) postulated a pre-Pangaea continent with austral and boreal zones adjacent to give account of the amphitropical distribution of many taxa. They emphasised that Diamesinae and Podonominae are a classic example of an amphitropically distributed group. Banarescu (1990, 1991) discussed the distribution of the aquatic insects and stated that many groups (Trichoptera and Diptera Blephariceridae for example) were present and widely distributed throughout Pangea. The analysis of the causes of the amphitropic distribution of Chironomid subfamilies is out of the scope of the present work, both the pre-Pangea or the Pangea hypothesis overrides the problem of a migration from Gondwana to Laurasia by dispersal and postulates a very ancient presence of Diamesinae in the Boreal regions. This means that the origin of Chironomidae should predate the breakage of Pangea: Chironomidae should have been widely distributed in Pangea before the Jurassic breakage of it. The austral-boreal disjunction of subfamilies should be a vicariance phenomenon, not a dispersion from south to north.

The analysis of the distribution of the tribes of Diamesinae within the Palaearctic region suggests the hypothesis that Boreoheptagyini never reached the British Isles and Scandinavia, whereas Protanypini never reached the Mediterranean area. This supports arguments in favour of a vicariant distribution of Boreoheptagyini in the south and Protanypini in the north of the Palaearctic region.

The tribe Diamesini is widespread in the Palaearctic. The analysis of the distribution of genera within the tribe shows that the most plesiomorph genus (*Pagastia*) is restricted to Siberia and Canada and does not reach Europe. This suggests an east-west vicariance within the tribe Diamesini. It is difficult to reconstruct the colonisation pattern within the Palaearctic, because different genera have their plesiomorph species in different provinces. The plesiomorph (?) genera *Pseudokiefferiella* and *Lappodiamesa* have a northern distribution, whereas the apomorph genera *Sympotthastia* and *Potthastia* are widespread. Because the relationships between these genera are still uncertain it is very difficult to formulate hypotheses.

When the distribution of species belonging to a group is analysed, it is often evident that the plesiomorph species have a southern area of distribution. This is true for many groups (*aberrata*, *latitarsis*, *zernyi*, *cinerella*) within the genus *Diamesa*. The straightforward explanation may be that during glacial epochs north Europe was devoid of fauna and the colonisation of northern provinces in post glacial periods was from the south.

Conclusions

The distribution of taxa within the Palaearctic region suggests that the process of colonisation is very ancient and goes back to a time preceding the breakage of Pangea. The model is that older branches of the phylogenetic tree (tribes) split in very ancient times (Mesozoic), whereas the younger ones split in Cenozoic (species within a species group in Pleistocene). Vicariance phenomena go back to Jurassic if the tribes distribution is considered, go back to Pleistocene if species distribution within a group is considered. The complete colonisation pattern of the subfamily followed many steps in different geological epochs and in each step the dispersion route had a different direction: south-north (Boreoheptagyini, Protanypini), east-west (*Pagastia* against other genera within Diamesini), north-south (*Pseudokiefferiella* + *Lappodiamesa* against *Diamesa*), south-north (different species within groups of *Diamesa*), west-east (species within *Symphottastia* and *Potthastia*). Many zoo-geographers (Jeannel 1942) state that colonisation of Europe became from the east, but this cannot be confirmed. Kownacki (1978) is convinced that the distribution centre of the *Diamesa steinböcki*-group are the mountains of Central Asia. The alternating glacial and interglacial periods enforces the hypothesis that the Palaearctic region was colonised repeatedly many times with different dispersion routes. This explains the species distribution within a species group.

Multivariate ordination methods suggest both an east-west and a south-north gradient of taxa, but the lack of taxonomy and distribution knowledge allows only main features be outlined.

Future needs are a better knowledge of phylogenetic relationships between genera to each other, between species within a species group and species distribution in critical areas (Himalaya, Siberia etc.).

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